

Structural and functional aspects of epiphytic and benthic algae in the acidified Lake Gårdsjön , Sweden

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STRUCTURAL AND FUNCTIONAL ASPECTS OF EPIPHYTIC AND BENTHIC

ALGAE IN THE ACIDIFIED LAKE GÅRDSJÖN, SWEDEN

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Structural and functional aspects of epiphytic and benthic algae in the acidified Lake Gårdsjön, Sweden

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The microstructure, distribution, taxonomic composition and primary production capacity of epiphytic and benthic algae were studied in an acidified lake.

The epiphytic cover on *Lobelia dortmanna* was made up of two distinct layers of epiphytes. Diatoms (*Eunotia*), bacteria and blue-green algae formed a firmly attached layer, which showed few seasonal changes in species composition. The loosely attached layer consisted of green algal filaments (*Mougeotia*, *Binuclearia*). This layer showed clear seasonal changes in species representation.

The benthic mat was built up of blue-green algal filaments (*Lyngbya*). Some species present in the filamentous matrix were also common in the epiphyton (*Merismopedia*).

Both algal assemblages contained mucilage. Most metals were found in the mucilaginous structures of epiphyton. Liming of the lake caused changes in the algal structures, favouring diatoms (*Achnanthes*) and

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förf. desmids. The primary productivity rates of epiphyton were highest at 1.0 m. Photosynthesis in the benthic

Förslag till ytterligare nyckelord

mat was restricted to the uppermost 2-3 mm.

Epiphyton, benthic mat, *Lobelia dortmanna*, acid lakes, limed lakes, primary production, colonization rates, blue-green algae, metals

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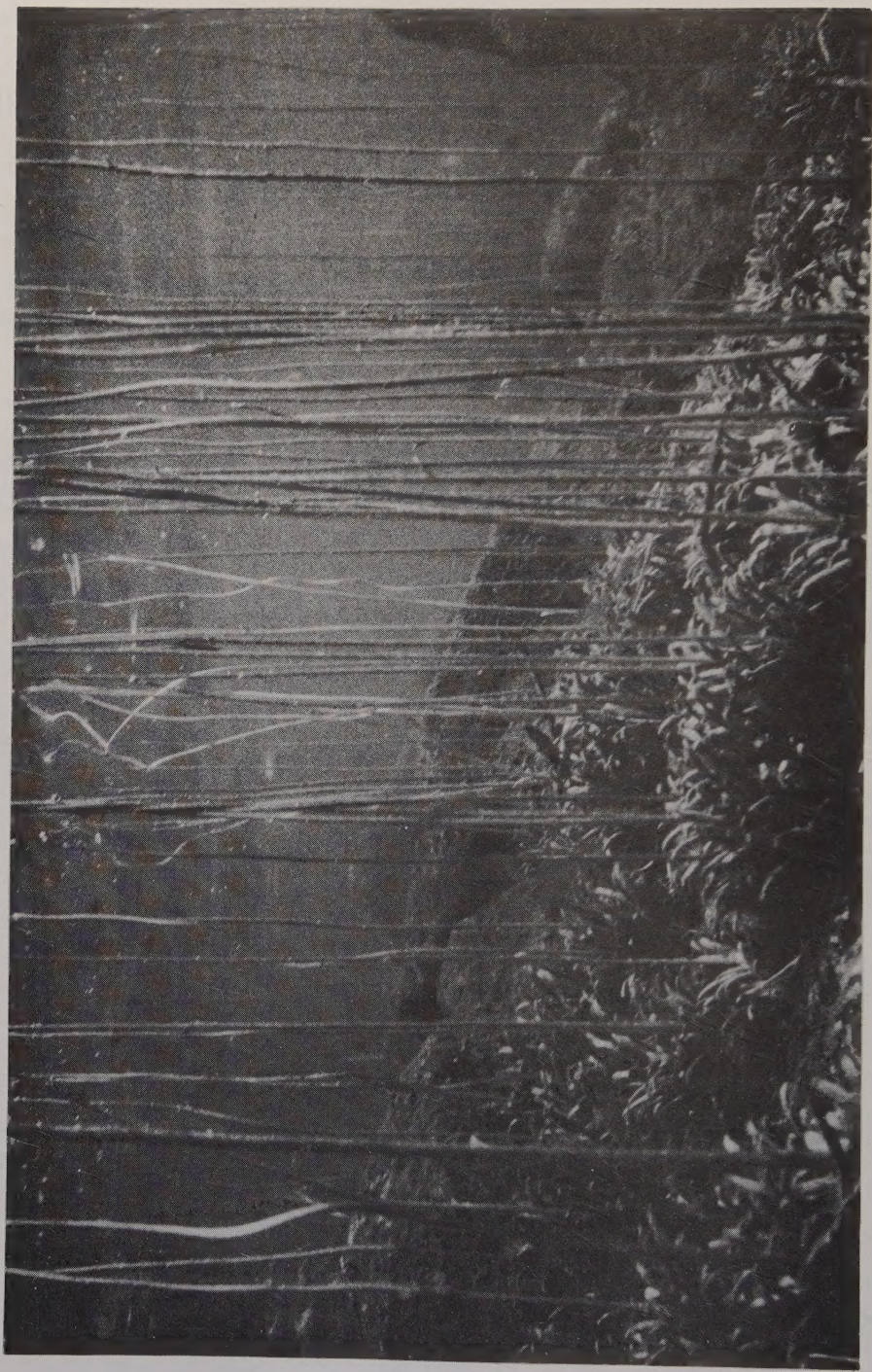
STRUCTURAL AND FUNCTIONAL ASPECTS OF EPIPHYTIC AND BENTHIC
ALGAE IN THE ACIDIFIED LAKE GÅRDSJÖN, SWEDEN

STANISLAW LAZAREK

DISSERTATION

Lund 1983

I do not know what I may appear to the world, but to myself I seem to have been only like a boy, playing on the seashore and diverting myself, in now and then finding a smoother pebble or a prettier shell than ordinary, while the great ocean of truth lay all undiscovered before me. SIR ISAAC NEWTON



View of the littoral in Lake Gårdsjön showing *Lobelia dortmanna* L. at 1.0 m.
Note the elongated stalks which bear the flowers above the water level.

PREFACE

Life may be unpredictable but events are not as unconnected as they seem. It is not hard to see how the first idyllic impressions of the ponds and meadows of my childhood gradually gave way to more inquiring, analytical observations. Yet, it is these memories which kindle the hope that the harmony between man and nature is not beyond restoration.

I am deeply indebted to the many people who befriended me, inspired me and helped me to see with new eyes. I would like to mention them all individually, but on this short page there is space only to name a few.

Maggan and Lasse Jonsson supported me loyally through thick and thin and opened their home and hearts to me without reservations. Dr Gunnar Andersson, never short of patience, was always ready with sound advice and open to discussion. Without him I may never have found my way out of the many bureaucratic labyrinths. Dr Wilhelm Granéli offered me help and friendship when it was most needed. I am grateful to Professor Sven Björk and my colleagues at the Institute of Limnology for accepting me and giving me the opportunity of proving myself.

I acknowledge Professor Brian Allanson for introducing me to the abstracts of the epiphytic microcosm and for emphasizing the stringent verification of results. I think warmly of my friend Dr Clive Howard-Williams. His generous and enthusiastic assistance extended beyond scientific necessities. Dr Jack Talling encouraged and supported me in my work. I thank my colleagues at Brookhaven National Laboratory for receiving me so warmly and for introducing me to the acidification problems in the Adirondacks. I am grateful for the kind assistance of the staff at the Section of Structural Zoology at the University of Lund.

Far from thinking that this work has exhausted the subject, I consider this as merely a good opportunity to critically revise and analyze my progresses and failures. I may therefore be permitted to hope that the ideas presented here provide the reader with some inspiration despite the obvious gaps in information and the sometimes faltering evidence.

This dissertation is dedicated to Thora.

LIST OF PAPERS

This thesis is based on the following published and unpublished papers:

- I. Structure and productivity of epiphytic algal communities on *Lobelia dortmanna* L. in acidified and limed lakes. *Water, Air, and Soil Pollution*, 18:333-342, 1982.
- II. Structure and function of a cyanophyten mat community in an acidified lake. *Canadian Journal of Botany*, 60:2235-2240, 1982.
- III. Microstructure and metal content of the *Lobelia*-epiphyte complex in acidified lakes. *Freshwater Biology*, accepted for publication, 1983.
- IV. Epiphytic algal production in the acidified Lake Gårdsjön, southwestern Sweden. *Ecological Bulletins (Stockholm)*, in press, 1983.
- V. Epiphytic colonization of *Lobelia dortmanna* L. in the acidified and limed Lake Gårdsjön, southwestern Sweden. Manuscript.

In the summary, the above Roman numerals will be used when referring to these papers.

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ABSTRACT

The microstructure, distribution, taxonomic composition and primary production capacity of epiphytic and benthic algae were studied in an acidified lake.

The epiphytic cover on *Lobelia dortmanna* was made up of two distinct layers of epiphytes. Diatoms (*Eunotia*), bacteria and blue-green algae formed a firmly attached layer, which showed few seasonal changes in species composition. The loosely attached layer consisted of green algal filaments (*Mougeotia*, *Binuclearia*). This layer showed clear seasonal changes in species representation.

The benthic mat was built up of blue-green algal filaments (*Lyngbya*). Some species present in the filamentous matrix were also common in the epiphyton (*Merismopedia*).

Both algal assemblages contained mucilage excreted by algae, which was important in the process of epiphytic attachment and in the consolidation of the benthic mat. Most metals found in the epiphytic cover were localized in the mucilaginous structures. Liming of the lake caused changes in the epiphytic structures and species composition, favouring diatoms (*Achnanthes*) and desmids. No such changes were observed in the benthic mat.

The productivity rates of epiphyton were highest at 1.0 m. The optimum conditions (light, availability of substrate and CO₂-content) for epiphytic production were found at 1.0 m. 14-C activity was higher in the firmly attached layer than in the loosely attached layer of epiphytes. Photosynthesis in the benthic mat was restricted to the uppermost 2-3 mm.

Use of the collodion technique and epiphyte-free *Lobelia* plants suggested their applicability to studies in acidified lakes.

SUMMARY OF RESULTS

INTRODUCTION

Wetzel & Allen (1972)*, illustrated the complex interactions between the various biotic and abiotic components of the littoral zone. The rôle of the littoral and its communities has been well-documented (Howard-Williams & Lenton, 1975; Mickle & Wetzel, 1978) as an inseparable part of the lake ecosystem.

Earlier descriptive studies of periphytic communities (e.g. Cholnoky, 1927; Godward, 1937) established a basis for today's more comprehensive approach.

Benthic algal microcommunities are more stable than are free-living communities (Moss, 1980). Their distribution is related to the availability and topography of adequately illuminated substrate (Talling, 1975). Benthic and epiphytic algae are less exposed to frequent light fluctuations than phytoplankton. The dead cells are not as easily sedimented as are those of free-living algae. This implies that nutrients which are released from the attached algae are recycled within the algal microcosm, providing an effective strategy of adaptation and survival in nutrient-poor conditions. Carignan & Kalff (1982) calculated that of the total amount of phosphorus recycled diurnally within the epiphyton, 90% originated from epiphytes.

A striking feature of benthic algae in acidified lakes in Scandinavia is the mat-like structural appearance.

*

Most references have been presented in the papers. Here I refer to the most relevant or to those which are not mentioned in the papers.

Environmental perturbations caused by acidification are reflected by structural and functional changes in the existing communities. The species diversity is low and the energy transfer between the various components of the lake ecosystem is less efficient than in undisturbed ecosystems.

A decline in the growth of macrophytes in lakes, specifically *Lobelia dortmanna* L. (van Dam & Kooyman-van Blokland, 1978), has been attributed to acidification. However, a gradual disappearance of *L. dortmanna* was reported earlier in Germany (Roll, 1939) - in connection with increasing eutrophication.

I allotted four years of study to illuminate some aspects of benthic and epiphytic algal structures and the production capacity of these algae in relation to environmental conditions. I concentrated on two representative and interacting algal assemblages present in the same microhabitat in the acidified Lake Gårdsjön*:

1) the epiphyton associated with *Lobelia dortmanna*.

2) the cyanophytan (blue-green algal) benthic mat.

I used *L. dortmanna* as a natural host-plant, to overcome problems resulting from the heterogeneity of the substrata. The plant is common in the littoral of the temperate oligotrophic lakes of northern Europe and northern America. Its morphological and physiological features made it suitable for my studies. Moon (1935) was the first to use trays with another isoetid, *Littorella*, for sampling the

* A map of Lake Gårdsjön showing the distribution of *Lobelia* and the sampling sites is presented in Appendix A. The environmental characteristics of the lake are presented in Appendix B and in the papers.

diverse communities in the littoral zones of the Lake District, England. I extended and elaborated his idea.

Recent studies of the ecology and physiology of *L. dortmanna* have been undertaken in the Netherlands (H. van Dam, personal communication) and in the United States at the University of Wisconsin-Madison (H. Boston, personal communication).

The benthic mat in L. Gårdsjön is a low diversity system made up of filamentous cyanophytes of the order Oscillatoriaceae. This highly controversial observation is interesting from a physiological and evolutionary point of view. Similar findings to mine from other parts of the world (e.g. Leupold, 1982; M. Leupold, personal communication), hint at an unknown pattern of biological adaptation to acid conditions.

It has been pointed out (e.g. Wetzel, 1975) that we too often attempt to describe the function of biological systems in terms of sophisticated mathematical formulas, neglecting the importance of contact with the living components of the system. I have tried to keep this in mind while providing detailed information on the structural properties of epiphytic and benthic algae and their production capacity.

I hope that the results presented here may be useful as a reference when we attempt to reverse the effects of acidification by liming acidified lakes.

STRUCTURAL ASPECTS

Species composition, Microstructure, Microdistribution, Content of elements (I,II,III,V).

Structural studies were performed in the spring, summer and autumn 1980, 1981 and 1982, at approximate monthly intervals. Scanning electron microscope (SEM) was used to determine the structural features of the epiphytic complex (I), the construction of the benthic cyanophytan mat (II) and a detailed survey of the *Lobelia* leaf surface with the patterns of epiphytic attachment (III). SEM was used in combination with an X-ray spectrometer to localize and check the relative content of some metals and phosphorus in the epiphytic complex (III). Transmission electron microscopy (TEM) was used to study bacterial colloidal products excreted during the attachment process (III). Microdistribution of the epiphytic cells was studied using a collodion impression technique (I,IV). The technique was elaborated (V) so that the firm epiphytic layer could be photographed at a magnification > X1000 and simultaneously, the cells could be counted under a phase-contrast microscope. The method proved particularly effective on *Lobelia* leaves but was also used successfully on *Nuphar* petioles, *Menyanthes* stalks and internodes of *Equisetum*. The collodion impression technique was used to study the epiphytic colonization of initially epiphyte-free surfaces. With this method, colonization rates, succession of species and the microdistribution of species could be investigated.

There are two types of benthic algae in L. Gårdsjön: the epiphytic algae associated with submerged vegetation, and the cyanophytan mat covering the sediment proper. A distinct flocculent mat composed of *Mougeotia* and

Binuclearia, forms an intermediate assemblage (metaphyton) in the warmer periods of the year (IV).

The epiphytic complex in L. Gårdsjön is a low diversity system. The values of the Shannon's index of diversity ranged from 0.31 to 0.76 in July-August, 1981, and in 1982 increased after liming in April, to between 0.64 and 1.20 in July-August. Some of the benthic species in L. Gårdsjön are presented in Appendix C.

The epiphytic complex associated with *Lobelia* consists of two layers of organisms which differ in their taxonomic composition, means of attachment, seasonal abundance and primary production capacity (IV).

The first layer is made up of the firmly attached diatom *Eunotia* with associated bacteria and colonial cyanophytes (I,III,V). After the liming of L. Gårdsjön, *Eunotia* gave way to the diatoms, *Achnanthes* and *Synedra* (V). This is consistent with an earlier observation from the limed reference lake, L. Högsjön, where these two diatom species dominated (I). There is evidence that *Achnanthes* and *Synedra* were abundant in L. Gårdsjön before it became acidified. The firmly attached layer contributed the highest percent to the total number of cells in the spring and winter (I,IV).

The second layer is built up of loosely attached green algae interwoven with bacteria, blue-green algae and diatoms. This layer could be removed by agitation. The seasonal changes in the species composition of the epiphyton were most apparent within the loosely attached fraction. The composition of the firm layer remained almost unchanged until 1982, when liming was performed.

Filamentous green algae (*Mougeotia*, *Binuclearia*) and blue-green algae were abundant in the summer (I,IV). The only abundant epiphytic desmid in L. Gårdsjön was *Penium*. After liming, the abundance and diversity of desmids increased (V).

The perennial benthic mat in L. Gårdsjön is composed of the motile filaments of two cyanophytan genera, *Lyngbya* and *Oscillatoria*. The occurrence of these two genera seems to have a local character, as the filamentous matrix of the benthic mat in a nearby lake, L. Hästevatten (pH 5.1-5.7) is composed of *Hapalosiphon* (II). *Lyngbya* and *Oscillatoria* were not present in the epiphyton. Several algal genera were represented in both the benthic mat and the epiphyton, e.g. *Merismopedia*, *Anomoeoneis*. Limited representation of invertebrates (nematods, chironomids) was encountered in both communities. Similar to the firm layer of epiphyton, the benthic mat did not show seasonal changes in the composition of the dominating species (II). After liming, the taxonomic composition of the epiphyton changed considerably, but so far no such changes have been observed in the benthic mat.

The epiphytic complex is built up on the epidermis of the *Lobelia* leaf, which is covered by a mucilaginous film (< 2 μm thick) of plant origin. The initial active settlement of rod-shaped bacteria and colonial cyanophytes is a rapid process, evident within one day (V). A passive attachment (mainly filamentous green algae and chain-forming diatoms) occurs on the barren leaves after a few hours of exposure (V). The development and function of the epiphytic complex and benthic mat is associated with the release of polysaccharideous material. The material is

important in the active attachment of cells and for the consolidation and protection of the algal assemblages against unfavourable environmental conditions (II,III). The epiphytic complex and benthic mat include sedimented detrital particles and entangled filaments of metaphytic algae with their associated bacteria.

The relative content of some metals in the epiphytic cover was estimated and they were localized in view of:

- 1) the high content of some metals in acid lakes and the possibility that a high metal content in the surviving algae limits grazing.
- 2) the possible connection to the high amounts of mucilage produced by algae in metal-contaminated, acid waters.
- 3) the impact of metals on algal metabolic processes, particularly photosynthesis.

The mucilage formations contained the greatest variety of metals and had the highest content of calcium, sodium and aluminium. The content of aluminium in the leaves of *Lobelia* with epiphytic cover was twice that in the leaves without cover. Biological uptake of aluminium by the firm layer of diatoms would explain this. Acid and metal resistant algal species appeared in L. Gårdsjön due to their structural and metabolic adaptation to a low pH environment (III). A chemical and physical modification of the existing microenvironment leads to the presence of low diversity, stable algal assemblages (II,III).

The successful experiments with epiphyte-free *Lobelia*-plants (V) suggest their applicability for monitoring the effects of acidification. The same set of plants may be exposed to different conditions in lakes and variations in the epiphytic structures may be compared. The collodion

impression technique offers a simple method of assessing the epiphytic cover without needing to remove the attached cells.

FUNCTIONAL ASPECTS

Biomass, chlorophyll a, primary productivity rates, primary production (I,II,IV).

The epiphytic and benthic algal production in L. Gårdsjön was estimated on the basis of *in situ* ^{14}C uptake experiments. The experiments were performed in 1980 and 1981 at 0.5, 1.0 and 2.0 m with the help of SCUBA diving. Several comparative measurements were carried out in two other acidified lakes in southwestern Sweden (I,IV). I built three types of plexiglas chambers (details are given in Appendix D), which were adjusted to the particular host-plant, type of lake bottom and community under investigation.

The daily light intensity was measured automatically at the side of the lake. In addition, the light intensity and light transmission were measured in the water during the ^{14}C incubation periods (Appendix E). 1 ml of $\text{NaH}^{14}\text{CO}_3$ (4 μCi , 1Ci= 37 GBq) was injected via a rubber septum. The period of incubation was either two or four hours. ^{14}C activity was determined on a liquid scintillation counter, and the concentration of dissolved inorganic carbon (DIC) in the water was determined in an IR Carbon Analyzer. To distinguish between bacterial and algal photosynthesis in the benthic mat, a photosystem II inhibitor (DCMU) was used (II).

Epiphytic biomass reached a maximum in the summer (1.0 mg

ash-free dry wt cm^{-2}). *Eunotia* had a stable biomass throughout the study period, while distinct seasonal changes in the biomass of the dominating loosely attached algae were noted (IV).

The highest chlorophyll *a* content was found in autumn ($3.4 \mu\text{g cm}^{-2}$). The mean chlorophyll *a* content in the benthic mat (II) was $81.3 \mu\text{g cm}^{-2}$. At a 1.0 m depth the epiphytic chlorophyll *a* values were not significantly correlated with the epiphytic productivity rates (I).

Productivity rates for the epiphyton associated with *Lobelia* compared favourably with reported values from other soft-water, nutrient-poor waters. I encountered the highest productivity rates in June 1980 ($1.0 \text{ mgC m}^{-2} \text{ hr}^{-1}$). Maximum daily productivity rates for the epiphyton on *Lobelia* were calculated in July 1981, as 69.6 mgC m^{-2} leaf surface area at a 1.0 m depth (IV). The daily productivity rates correlated best with the stable biomass of the tightly attached fraction of algae (IV). Higher daily productivity rates were found for the epiphyton associated with *Isoetes* and *Nuphar*. However, due to the fact that *Lobelia* is the dominating macrophyte in the lake (Appendix B), it provides the largest biotic substrate area available to epiphytic colonization. The mean daily productivity rate in the benthic mat was equal to 32.8 mgC m^{-2} . The photic zone in the mat is restricted to the uppermost 2-3 mm.

The annual production of epiphyton on *Lobelia* was 1.8 gC m^{-2} leaf surface area. This value corresponds to the extremely low values reported for epiphytic production in soft-water lakes.

It was not possible to establish the total annual primary

production of the lake, as the annual production of the cyanophytan mat and the metaphyton in the lake has not been estimated. This requires detailed knowledge of the seasonal and daily changes in the CO_2 turnover and the light conditions at the bottom of the lake, as well as information on the distribution of these communities.

The DIC content in the water was highest at 0.5 m, declining with depth. Liming caused an eightfold increase in the DIC content in the water. This should have a positive long-term effect on primary production in the lake.

PERSPECTIVES

The results I have presented suggest several questions which would be rewarding to tackle in future research on benthic algae. Some of the following problems are of immediate practical importance for acidified waters, others are of value in theoretical limnology. Here are some aspects I would particularly like to elaborate on in future investigations:

- 1) The experimental manipulation of epiphyte-free *Lobelia* plants has afforded promising possibilities for continued studies on the epiphytic colonization of *Lobelia* and other macrophytes. Experiments may be performed in lakes with different physico-chemical conditions. Epiphytic communities could be subjected to certain grazers in a given period and the effect of grazing on the epiphytic structures could be compared in the laboratory and under natural conditions. The energy value (protein content) of the algal material could be determined.

- 2) Sediments from various acidified lakes could be inoculated with blue-green algae and the pattern of colonization, the physical structure of the developing cover, the succession of species and the physico-chemical modifications of the sediment-water interface could be followed.
- 3) ¹⁴C track autoradiography could be used to determine the production capacity of individual acid-resistant algae under controlled light conditions. Studies of this kind will be initiated later this year during my stay at the University of Toronto, Canada.
- 4) The mechanisms regulating the formation of green algal clusters in the littoral of acidified lakes should be established, and the impact of these formations on the rates of nutrient diffusion from the sediment to the water should be determined.
- 5) Studies on the physiology of species such as *Mougeotia*, *Binuclearia*, *Batrachospermum* and *Zygnema* should be intensified.

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EPIPHYTIC COLONIZATION OF *LOBELIA DORTMANNA* L. IN THE
ACIDIFIED AND LIMED LAKE GÅRDSJÖN, SOUTHWESTERN SWEDEN

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Summary

An experiment on the epiphytic colonization of epiphyte-free *Lobelia* plants was performed in 1981, in the acidified Lake Gårdsjön, Sweden. The experiment was repeated in 1982, four months after liming of the lake.

Colonization of the barren leaf surfaces was rapid. The process was initiated (after one day), by a passive attachment of algal cells (*Mougeotia*, *Tabellaria*) and an active attachment of bacteria. After four weeks of exposure the epiphytic structures that had developed were similar to the epiphytic structures associated with *Lobelia* growing naturally in L. Gårdsjön.

Liming resulted in the replacement of *Eunotia* in the firm layer of epiphyton, by *Achnanthes* and *Synedra*. The recruitment of new species was most evident in the loose layer of epiphyton. The new species that appeared were represented by desmids, diatoms and filamentous bacteria.

The diversity indices of epiphyton had low values due to the domination of a few taxa. The epiphytic structures that developed before and after the liming, shared 68.4% of the maximum community similarity.

EPIPHYTIC COLONIZATION OF *LOBELIA DORTMANNA* L. IN THE ACIDIFIED AND LIMED LAKE GÅRDSJÖN, SOUTHWESTERN SWEDEN

S. Lazarek

Introduction

The development of the periphytic community in eutrophic conditions resembles the successional stages in the development of higher plant communities (Hoagland *et al.* 1982). Jordan & Staley (1976) pointed out the significance of heterotrophic bacterial attachment in the initial stage of periphytic colonization in Lake Washington. Both these studies stressed the importance of the morphological structures of attaching microorganisms for successful colonization of bare substrates. This includes their extracellular polysaccharideous products.

It was suggested that the addition of lime to the water of an acidified lake introduces structural changes in the existing *Lobelia*-epiphyte complex without increasing the primary production capacity of the complex (Lazarek, 1982). The replacement and recruitment of new algal species were observed after the liming had been performed. Further, it was noted (Lazarek, 1983a) that the production of mucilage, which is important for nutrition, attachment and consolidation of the epiphytic complex, was higher in low pH conditions.

Liming of the acidified Lake Gårdsjön, created an excellent opportunity of carrying out simple short-term experiments where the epiphytic colonization and its

successional stages could be followed before and after the addition of lime.

My intention was to quantify the successional stages of the developing epiphytic cover in terms of species diversity, dominance and biomass, with special attention paid to the initial step of the colonization process. This study was primarily designed to monitor the structural reorganization of epiphyton in response to the environmental perturbation which liming of the lake caused.

The notorious problems arising from the heterogeneity of substrates and the separation of attached microorganisms from substrates have brought about the adoption of artificial substrate sampling techniques, as Müller (1980) and Stokes (1982) have demonstrated in their investigations of the acid impact on lakes. A modern approach to the problems related to sampling with artificial substrates was provided by Cairns (1982).

In this study, I used the land-form of *Lobelia dortmanna* L. which was first reported in Sweden by Sylven (1903) and in Germany by Hoepfner (1932). The idea of using epiphyte-free land forms of aquatic plants for studies of epiphyton was introduced by Brown (1974) but has so far not been given the attention it warrants.

Material and Methods

a) *material*

The experiments were performed in Lake Gårdsjön, south-western Sweden. A map of L. Gårdsjön showing the distribution of *Lobelia* and the sampling sites, is presented together with information about the limnology of the lake in Appendix A and B of the thesis.

Land forms of *Lobelia* were collected from the eulittoral of L. Gårdsjön and planted in plastic flower pots in sand from the lake. The pots were kept in aquaria with the water level reaching half-way up the sides of the pots. After three months of acclimatization in a green-house, the pots were re-transferred to L. Gårdsjön. Before starting the experiments, the leaves of the plants were carefully washed using filtered water to remove any microorganisms that could have developed on the leaf surface while the plants were in the aquaria.

Five pairs of *Lobelia* plants (in their pots) were embedded in the sand on the bottom of the lake at a depth of 0.5 m, at the end of July 1981, and exposed to epiphytic colonization for about four weeks. One pair of plants was sampled the following day to check for the presence of pioneer organisms. One pair of plants was collected each week and the plants were kept separately in jars with formalin-aceto-alcohol fixative (Grimstone & Skaer, 1972). The experiments were repeated in 1982, from the end of July through August. L. Gårdsjön had been limed in April 1982.

b) *microscopic analyses of algae*

Analyses began at the end of August, after all the plants had been collected. The total number of leaves on each

plant ranged from 12 to 25. Only healthy leaves were taken for analyzing species composition and abundance of epiphytic cells. The abundance of organisms was determined on the basis of their number of cells per cm^2 of the leaf surface area. The cells were counted in the following way:

Two leaves from the same plant were placed in separate vials with two milliliters of distilled water and shaken vigorously about 100 times. The algal fraction which became detached is referred to as 'loosely attached' algae (analysed on Sedgwick-Rafter counting cell), while the remaining cells comprise the 'tightly attached' assemblage (Cattaneo & Kalff, 1978) analysed by the collodion film method. These two fractions were treated separately.

The suspension of loosely attached algae was transferred to two Sedgwick-Rafter counting cells (S-R). The recommended (Woelkerling *et al.*, 1976) settling time was 10 mins. The cells were counted at a magnification of X250. Five to ten fields on two S-R cells were counted along the transversal and longitudinal axes. Results were transformed to numbers of cells per cm^2 of the surface area of the *Lobelia* leaf, determined planimetrically.

The values presented in Table I were used to check the precision of the method. The method was tested using the Kolmogorov-Smirnov two-sample test (Siegel, 1956, p. 127-136). The largest discrepancy (K_D) between scores on A and B cells, was equal to 2. At this value ($\alpha = .01$ of the two-tailed K.S. test) the null hypothesis that scores obtained on the two S-R cells represent the same population, could not be rejected. The total number of cells per cm^2 of the leaf surface area consists of mean estimates on both sides of the leaf.

TABLE I. The comparative counting of diatoms in samples from five different *Lobelia* leaves was performed simultaneously on two S-R cells (designated as A and B).

leaves	I	II	III	IV	V
A	680	850	3000	2500	120
B	1100	300	450	2350	100

Scanning electron microscopy (SEM) and epifluorescence techniques could not be used routinely in this work, due to financial and accessibility difficulties. Not wanting to lose the information inherent in the undisturbed patterns of the epiphytic microdistribution, I applied the collodion film technique first suggested by Wenzl (1940) for fungal epiphyll studies. Margalef (1949) used the method for studying aquatic attached communities. The procedures were the following:

The leaf was dehydrated in a series of ethanol and diethyl ether for about 30 mins. It was stained with 5% iron haematoxylin (Grimstone & Skaer, 1972) and then submerged for a few secs in 4% collodion (E. Merck, Darmstadt) dissolved in ethanol (96%) and ether. The transparent film (about 50 μm thick) which formed after drying was peeled off the leaf. The effectiveness of the method was checked by repeatedly covering the leaf with collodion and then examining the film obtained under a microscope. Cells were removed to almost 100% by the first application of collodion. A few mm^2 of the film from both sides of the *Lobelia* leaf was placed on the microscope slide with a drop of Histoclad synthetic microscopic mounting medium (Clay Adams, Parsippany, N.J., refractive index = 1.54). Due to

the thickness of the film and its transparency, high-contrast micrographs could be taken at a magnification of X1250. The sides of the leaf were easily recognizable by the presence or absence of stomata impressions in the film.

Similar techniques were described by Dickinson *et al.* (1974) who used cellulose film for the removal of bacterial epiphyton, and by Cattaneo (1978) who used a cosmetic 'facial mask' to peel epiphytes off leaves. Cosmetic film could not be satisfactorily applied in my work because it gave a highly granulated background on micrographs taken at magnifications > X500, which severely hindered the counting of bacteria.

The embedded diatoms and pseudofilamentous blue-green algae were counted with the help of a Whipple ocular reticule which is divided into fields arranged in blocks. One block consists of 25 fields. The number of blocks which were counted depended on the density of the epiphytic cover. Microdistribution of the epiphytic cells was also registered on micrographs taken under a phase-contrast microscope and, in some cases under a scanning electron microscope (SEM).

c) analysis of bacteria and filamentous blue-green algae.

Bacteria and filamentous blue-green algae were counted with the help of the collodion film impressions of the leaves which contained tightly attached epiphytes. It was technically possible to count the organisms which formed distinct colonies or filaments. Bacteria were counted from the collodion film impressions, as the configuration of the S-R cell inhibits the use of a high-power microscope objective making identification of organisms smaller than 15 μm ~~was~~ difficult or impossible. The procedures were as

follows:

Several bacterial colonies on randomly chosen parts of the collodion film from five leaves were photographed at X1250, using an immersion oil objective. This gave an estimation of the average number of bacteria per colony for each of the sampling days. All the micrographs were taken with ILFORD PANF 50 ASA black and white film.

To calculate the number of bacteria per cm^2 of leaf surface area, the same collodion film impressions were viewed under X1000 magnification and the number of microcolonies on randomly selected microscope fields was counted.

The filamentous algae appeared on the first day of colonization, almost exclusively in the loosely attached fraction. In order to count the filaments accurately, I modified the Burnham *et al.* (1973) method as follows:

The total length of any filament was tallied on 50 randomly selected fields from the 1000 fields of a S-R cell at a magnification of X250. This was designated as C. The number of cells per 50 μm of the filament was calculated under a phase-contrast microscope, using a magnification of X1000. This was designated as B. The mean number of cells per field of the S-R cell (A) was found using the equation $A = C \cdot B / 2500$. By multiplying A by 1000 the number of cells per 1 ml (the volume of S-R cell) was obtained. This value was then transformed to number of cells per cm^2 of the leaf surface area.

All stages of counting on S-R cells were performed under a Reichert light microscope, while a phase-contrast

ORTHOLUX microscope was used for the remaining analyses and for taking the micrographs.

d) *diversity statistics*

I used the simplest measure of diversity, the Shannon-Wiener function

$$DI = - \sum_{i=1}^S p_i \log p_i, \text{ (Pielou, 1977)}$$

To obtain a representative sample of the population, 200 organisms were counted on the first day of colonization, and from 1000 to 2000 individuals on the subsequent sampling dates. For bacteria, morphological type of cell was assumed to be equivalent to species (Jordan & Staley, 1976) and one bacterial colony was considered as an individual.

The species evenness index was calculated as $J = DI / \log S$ where DI is the index of diversity and S stands for number of species (Marcus, 1980).

A quantitative comparison of epiphytic communities was made using a similarity index $SIMI$ (McIntire & Moore, 1977) calculated as:

$$SIMI = \frac{\sum_{i=1}^S P_{ai} P_{bi}}{\sqrt{\sum_{i=1}^S P_{ai}^2} \sqrt{\sum_{i=1}^S P_{bi}^2}}$$

$SIMI$ is the measure of similarity between the communities on the corresponding days in 1981(a) and 1982 (b), where P_{ai} and P_{bi} represent proportions of individuals represented by i -th species in 1981 and 1982 respectively. S stands for the total number of species in the two communities. $SIMI$ has a minimum value of 0 when the two compared communities had have no species in common, and a maximum value of 1 when their species composition and proportions were identical.

Results

The average daily surface water temperature during the experiments (July-August) ranged from 16.5°C to 19.0°C in 1981, and from 19.5°C to 22.5°C in 1982. In 1981, the pH was 4.6 and after liming, in 1982, the pH increased to 7.6.

In both years, filamentous and chain-forming organisms predominated in the initial stage of epiphytic succession. The percentage of cells shared by the six dominating and/or characteristic (present in all samples) taxa on the exposed leaves, ranged from 77% to 86% in 1981 (Fig. 1A). In 1982, the number of dominating algal taxa increased from three on the first day, to six, in the fourth week of exposure. Pooled, the contribution of the dominating taxa to the total amount of settled cells ranged from 91% on the first day to 93.5% at the end of the experiment (Fig. 1B).

The six dominating taxa made up 86.5% in July to 98% in August 1981, of the total number of cells on the naturally growing plants (Fig. 2). The values for the corresponding months in 1982 ranged from 91.5% to 88.5%.

In both years, filamentous Chlorophyceae *Mougeotia* sp., *Oedogonium* spp., and the chain-forming diatom *Tabellaria flocculosa* (Roth) Kütz. appeared on the first day of exposure. *Tabellaria* showed little change in abundance ($0.5 \cdot 10^4$ to $2.7 \cdot 10^4$, $\bar{x} = 1.4 \cdot 10^4$ cells cm^{-2}). Its relative contribution to the total number of cells declined progressively during the experimental period, due to the settlement of unicellular algae.

In 1981, *Dinobryon divergens* Imhof. was an important component of the epiphytic biomass. It constituted 10% of the total number of cells on the first day, and 28% after

three weeks of exposure. On naturally growing *Lobelia* it ranged from 2.5% in July to 28.5% in August, 1981. The contribution of *Dinobryon* and *Oedogonium* in 1982 was negligible.

In 1982, the firmly attached diatom *Eunotia** (Fig. 4A-B) which dominated in 1981, declined and was succeeded by the two codominant genera *Achnanthes* and *Synedra* (Fig. 4C-D). *Achnanthes* was not found on *Lobelia* after one day of exposure, but then the number of cells increased rapidly (Fig. 1B), reaching a maximum after two weeks ($4.0 \cdot 10^4$ cells cm^{-2}). On naturally growing *Lobelia*, the number of *Achnanthes* cells ranged from $4.0 \cdot 10^4$ in July, 1982, to $2.4 \cdot 10^5$ cells cm^{-2} in August, 1982.

In the 1981 experiment, *Eunotia* contributed 2%-33% of the total number of cells. In 1982, its contribution was reduced to only 2.5% at the end of the experiment. On naturally growing *Lobelia*, it still made up from 11% in July to 24% in August, 1982, compared to 33% and 27% for the corresponding months in 1981.

The Spaerman rank correlation test, run on untransformed variables, indicated a significant disparity in the microdistribution of the two diatoms, *Achnanthes* and *Eunotia* (Fig. 3). *Achnanthes* was significantly more abundant on the lower side of the leaf ($r_s = 0.33$, $p = 0.05$). *Eunotia* showed a clear preference for settling on the upper side of the leaf ($r_s = 0.75$, $p = 0.05$).

* Based on the morphological similarities (cf. van Dam et al. 1981), in the text below, *Eunotia* refers to *E. rhomboidea* and *E. veneris*, and *Achnanthes* to *A. microcephala* and *A. minutissima*.

The settlement of bacteria on exposed leaf surfaces was a rapid process owing to the morphology of the organisms. Only rod-shaped microorganisms could be recognized in the collodion film peeled off leaves incubated for one day in 1981 (Table II). The numbers of microorganisms were considered significantly different when their 95% confidence limits did not overlap. The density of rod-shaped organisms increased in the first week of exposure in 1981, after which the numbers stabilized. Rods were significantly more abundant in 1981, when the average number of cells per colony in the third week of exposure was 18.

Distinct microcolonies of coccoids appeared on the leaf surface among the already settled *Eunotia* (Fig. 4A) within one week in 1981. The density of coccoids increased continuously during the three weeks of exposure (Table II), with the number of cells per colony ranging from 10 to 50. No filamentous bacteria were observed in 1981.

In 1982, three morphological types of bacteria were represented from the first day of exposure (Table II). The density of coccoids was significantly higher in the first two weeks than it had been in the same period in 1981. The number of cells per colony ranged from 12 to 80. Rod-shaped organisms were significantly less abundant in 1982, although there were more cells per colony than in 1981 (12 to 40, compared with 4 to 18).

In 1981, the blue-green algae *Tetrachloris* sp. (Fig. 4B), probably *T. merismopedioides* Skuja, and *Aphanothece* appeared on the exposed leaves on the first day. In both experiments, the size of the colonies of *Aphanothece elabens* (Bréb.) Elenkin and *A. stagnina* (Spreng.) A. Br.

(Fig. 4E) increased rapidly. *Aphanothece* appeared in significantly higher numbers in 1981 than in 1982. *Tetrachloris* was not present in the 1982 samples. In 1982, *Pseudoanabaena* sp., *Gloeocapsa* sp. and filamentous bacteria resembling *Vitreoscilla* sp. (Godinho-Orlandi & Jones, 1981) were observed on initially epiphyte-free leaves. The pseudofilamentous blue-green alga (*Johannesbaptistia* sp., R.N. Nordin, personal communication) shown on Fig. 4F, appeared in the firmly attached layer of epiphytes in the 1981 experiment. This little known microorganism was a characteristic component of the firm layer of epiphyton in the lake before liming.

Few species were represented on the exposed leaves during the four weeks of exposure and the number of species was similar in both years (Table III). The structure of the epiphyton by the fourth week resembled that of the naturally existing assemblages. In both years, the highest number of epiphytic taxa on the naturally growing *Lobelia* was found in July. Fifteen taxa were common in the pooled samples of the epiphyton from naturally growing *Lobelia*, in July and August 1981 and 1982. On exposed plants, six taxa were common for the epiphyton developing after one day of exposure in 1981 and 1982.

The diversity and evenness indices (Table III) show similarly low values for both experimental periods. A continuous increase in diversity values was noted in the 1981 experiment, while in 1982 the values were less consistent. The number of taxa common to both experimental periods increased to eight by the fourth week. Most other taxa occurred occasionally and in low numbers.

The calculated similarity values ranged from 0.488 to

0.727. Comparison of the *SIMI* values for the epiphytic structures that developed in 1981 and 1982, revealed that they shared 68.4% of the maximum similarity (Table III).

Some new species appeared on naturally growing *Lobelia* in 1982 (Table IV). These were represented mainly by desmids and diatoms. The recruitment of new species was more pronounced in the loosely attached fraction of epiphyton, but as these species appeared in low numbers they had little effect on the similarity and diversity indices.

So far, there is little evidence that any epiphytic taxa disappeared after liming. *Binuclearia* had been an important component of the epiphytic and metaphytic biomass in the lake before liming (Lazarek, 1983b), but five months after liming only a few cells were found.

Discussion

Epiphytic colonization was rapid even in extremely oligotrophic conditions and at low pH levels. The initial stage of epiphytic colonization in both experiments could be described as: a) passive entanglement of "pioneer" algal organisms such as *Mougeotia* and *Tabellaria*. This process was probably determined by the morphological features of the settling organisms and their abundance in the littoral, and by water movement. b) active attachment of bacterial cells by means of mucilaginous strings (Lazarek, 1983a). The collodion technique revealed that coccoidal cells colonized those areas of the leaf surface that were free of epiphytes. This technique also allowed for observing the compact bacterial microcolonies that must have originated from a settled single cell. The growth of coccoidal microorganisms

on *Eunotia* frustules (Lazarek, 1983a) must have occurred at a later stage of epiphytic development.

Later colonization was characterized by: a) passive attachment of diatoms, which subsequently developed specialized modes of attachment e.g. flattened mucilaginous adhesive around the lower valves (*Eunotia*) or mucilaginous stalks (*Achnanthes*) and pads (*Synedra*). b) passive attachment of colonial blue-green algae (*Merismopedia*, *Tetrachloris*) and desmids. This process was largely mediated by the topography of the leaf surface and the presence of organic substances released by previously settled epiphytes (Lazarek, 1983a).

The principal criteria for comparing the epiphyton that developed before and after liming were: 1) taxonomic composition. 2) the sequence of the species in the colonization process. The influence of light, believed to determine the taxonomic composition of epiphyton (Brown, 1976), was minimized by performing the experiments at the same depth.

The addition of lime influenced the taxonomic composition of epiphyton, as some algal organisms were eliminated and new algae were recruited. These processes were clearly observed on the exposed *Lobelia* but were less evident on the naturally growing plants. This may indicate that environmental conditions did not have the same effect on the naturally existing epiphytic assemblages as on the developing epiphyton.

The structural reorganization of the existing epiphytic assemblages was much slower than on the newly colonized surfaces. It is notable that *Eunotia*, three months after

the experiment in 1982, remained the dominating component of the firm layer of epiphyton on naturally growing *Lobelia*. On the initially epiphyte-free leaves, *Eunotia* was rapidly exchanged for *Achnanthes* and *Synedra*. Paleolimnological studies by Renberg & Hellberg (1982) showed that these two diatoms were present in the lake before the acidification process began. The reappearance of the diatoms is one of the most evident biological effects of liming. The qualitative pattern of changes induced by liming seems consistent with earlier observations from the limed Lake Högsjön (Lazarek, 1982). Moore (1977) noticed that *Achnanthes* has several physiological forms and suggested that this contributes to a high adaptability. The number of cells in the *Eunotia* population increased slowly but continuously, while the number of *Achnanthes* cells decreased slightly in the two weeks following exposure in 1982. This may indicate competition for space which resulted in the mechanical removal of *Achnanthes* by the growing cells of *Eunotia*.

With the collodion film technique, it was possible to quantitatively assess microdistribution of *Eunotia* and *Achnanthes* on the *Lobelia* leaves. Differences in the abundance of these diatoms on the upper and lower sides of the leaf may be attributed to light preference or differences in the metabolism of the upper and lower sides. Cattaneo (1978) found *Eunotia* species more abundant on the lower sides of *Potamogeton* leaves. She related these differences to the metabolism of the host-plant. Düringer (1958) observed a preference in diatoms for colonizing leaf edges. He proposed that this is due to more favourable illumination and nutrient renewal in these areas.

It was noted in both experiments that the firm layer of

epiphytes after the initial fast growth, did not change in taxonomic composition and that the biomass tended to stabilize.

The recruitment of new species of desmids was another visible effect of liming, consistent with observations in Lake Högsjön (Lazarek, 1982). The increase in pH and the content of DIC (from 1.0 to 8.0 mg l⁻¹) in the water seems to favour desmids. Coesel (1978) puts forward an idea of decreasing diversity of desmids in waters exposed to acidification and oligotrophication. He observed the replacement of desmids by a uniform, excessive development of blue-green algae. Higher abundance of some blue-green algae, particularly *Aphanothece*, *Merismopedia* and *Tetrachloris*, in the 1981 experiment supports Coesel's observations. Moss (1973), discussing factors associated with exclusion of oligotrophic algae from eutrophic waters, considered the following factors important: a) direct effect of pH on the enzyme system of algae. b) toxic effect of CO₃²⁻ or OH⁻ ions. c) the availability of different DIC compounds for photosynthesis which most reasonably explained his laboratory and field observations.

In both experiments, the diversity indices were low due to the domination of a few species. The epiphytic complex that developed after four weeks of colonization can, to some extent, be considered a 'stable system' as it consisted of organisms representing various forms of metabolism. The complexity of the epiphytic structures increased to a certain level, after which the structural parameters such as biomass and diversity stabilized.

The collodion film technique proved to be a practical alternative to SEM techniques which are expensive and

laborious, and cannot be applied in routine studies. Additionally, the use of SEM to observe bacteria is limited (Jordan & Staley, 1976) and the natural distribution of microcolonies may be disturbed by fixing procedures. However the collodion film technique cannot be applied on fragile and old leaves that support heavy epiphytic covers.

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TABLE III. Indices for the epiphyton on naturally growing *Lobelia* plants (N) and for the epiphyton which developed on initially epiphyte-free *Lobelia* plants, exposed for from 1 to 28 days in the L. Gårdsjön experiments. Number of taxa (*S*), diversity (*DI*), median value of the similarity index (*SIMI*) and the evenness index (*J*) are given. The median value of the similarity is derived from the *SIMI* values for the corresponding dates in 1981 and 1982.

	N	1981			N			1982			N			
		1	7	14	21	28	August	July	1	7		14	21	28
<i>S</i>	28	12	22	19	20	19	18	26	8	20	20	16	21	22
<i>DI</i>	0.31	0.25	0.58	0.98	1.30	1.12	0.76	0.64	0.78	0.85	0.66	1.04	0.91	1.20
<i>SIMI</i>	0.684													
<i>J</i>	0.21	0.23	0.43	0.77	1.00	0.88	0.60	0.45	0.87	0.65	0.51	0.87	0.69	0.90

0.684

TABLE IV. Some characteristic algal species, not observed in 1979-1981, which appeared on the naturally growing *Lobelia* plants in L. Gårdsjön in 1982.

Scenedesmus serratus (Corda) Bohl.

Cosmarium phaseolus Bréb.

Docidium undulatum Bail.

Gonatozygon Brébissonii West & G.S. West

Xanthidium antilopeum (Bréb.) Kütz.

Achnanthes microcephala (Kütz.) Grun.

A. minutissima Kütz.

Neidium bisulcatum (Lagerst.) Cl.

Synedra ulna (Nitzsch) Ehrenb.

Figure 1. Trends in relative abundance of the dominating and/or characteristic taxa on initially epiphyte-free *Lobelia* leaves exposed to colonization for from 1 to 28 days in L. Gårdsjön in 1981 (A) and in 1982 (B). Percentage contribution was estimated using the number of cells of a particular taxa and the total number of algal cells. Bacteria and blue-green algae are not included.

Figure 2. Relative abundance of the dominating and/or characteristic taxa of epiphytic algae on the leaves of naturally growing *Lobelia* in L. Gårdsjön. Diagrams represent the composition of the epiphytic communities sampled at the start and end of the colonization experiments at the same sampling site in 1981 and 1982. Bacteria and blue-green algae are not included.

Figure 3. Logarithmic histogram showing the distribution of the diatoms *Achnanthes* and *Eunotia* on the upper and lower sides of initially epiphyte-free leaves of *Lobelia*, exposed to colonization in L. Gårdsjön, July-August 1982. Bars are enclosed by their corresponding ranges.

Figure 4. Some components of the epiphytic cover which developed on *Lobelia* in L. Gårdsjön, 1981 and 1982. A, B, C, E and F are LM micrographs. D is a SEM micrograph.

A) Collodion film with *Eunotia* and coccoidal microorganisms on the 7th day of colonization, 1981.

B) Collodion film with *Eunotia* (e), *Tetrachloris* (t), rod-shaped (r) and coccoidal (c)

microorganisms on the 7th day of colonization, 1981.

C) Collodion film with *Achnanthes* (a) and *Synedra* (s), 14th day of colonization, 1982. Note: mucilaginous stalks (arrows).

D) Cells of *Achnanthes* attached to the barren surface of a *Lobelia* leaf on the 7th day of colonization, 1982. Note: mucilaginous stalk (arrow).

E) Collodion film with a colony of *Aphanothece*, 14th day of colonization, 1982.

F) Pseudofilamentous blue-green alga in the collodion film, photographed under a phase-contrast microscope with a Whipple ocular placed in the tubus.

Fig. 1A

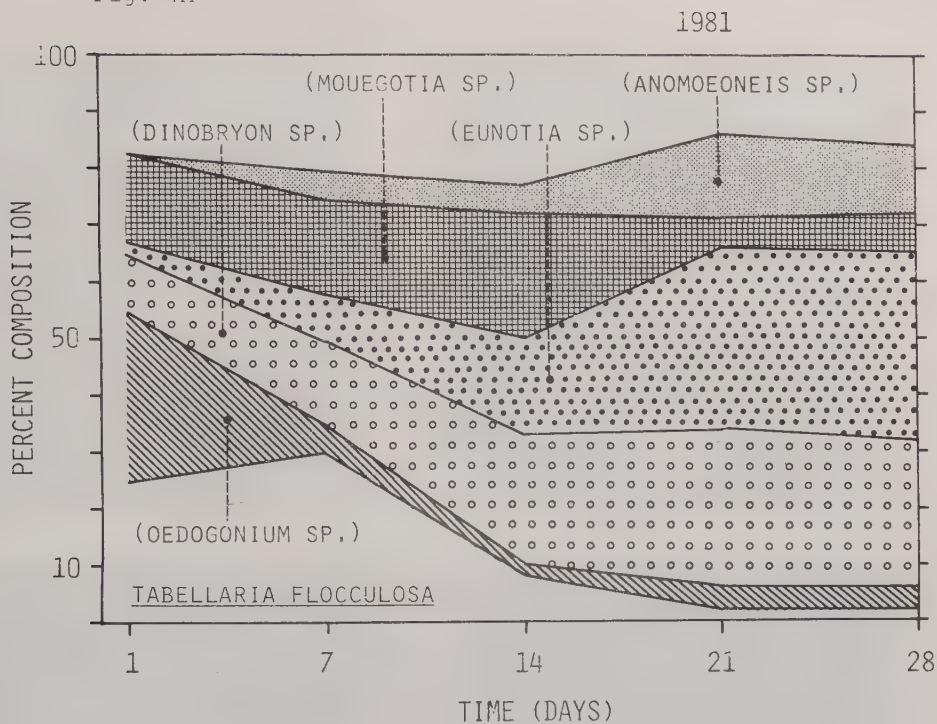


Fig. 1B

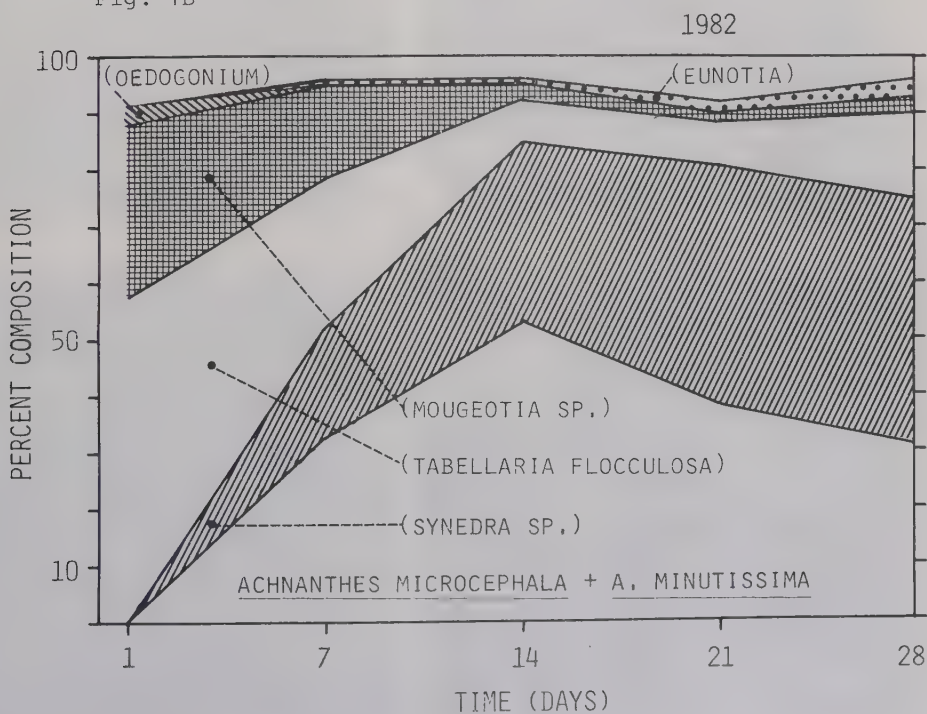


Fig. 2.

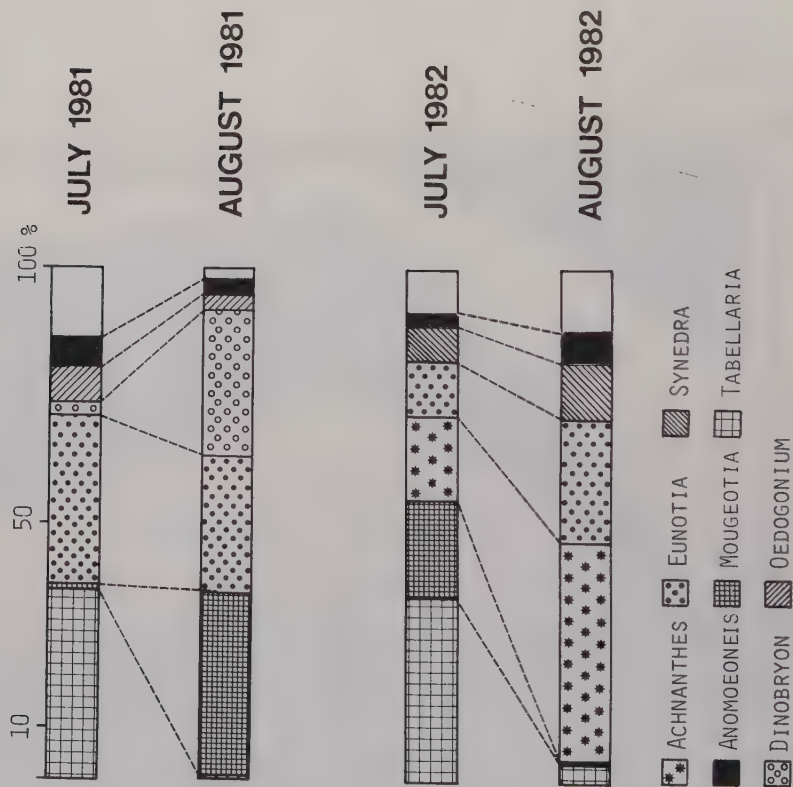


Fig. 3.

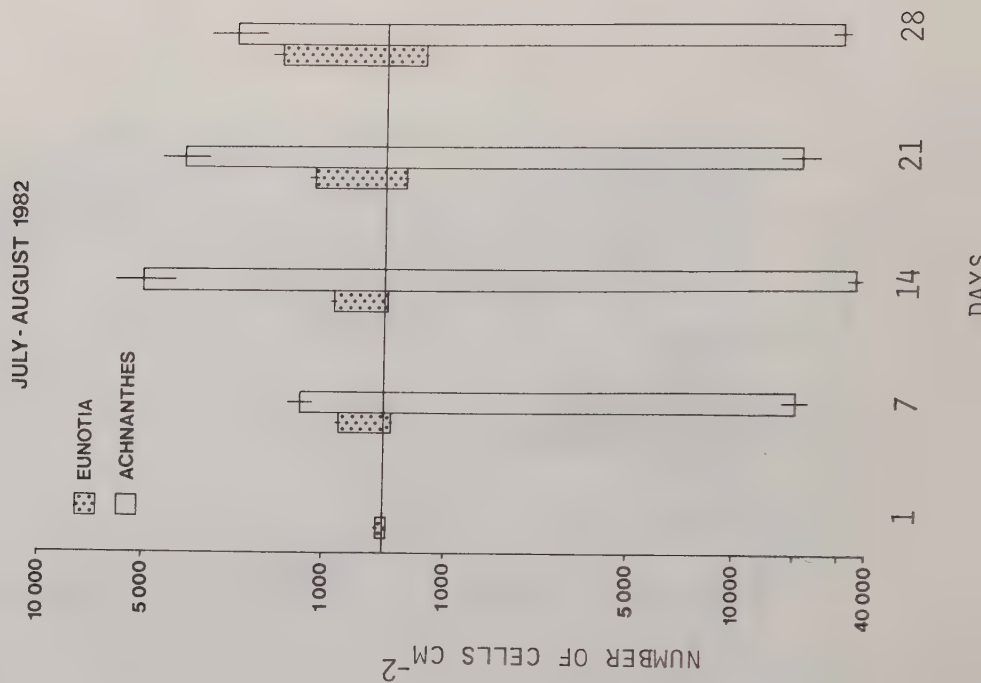
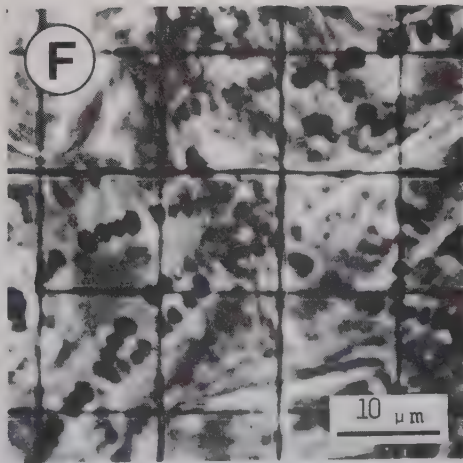
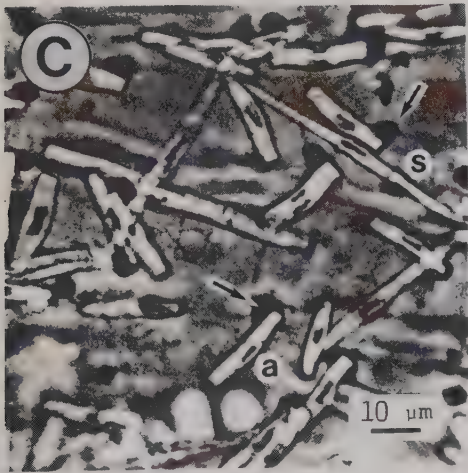
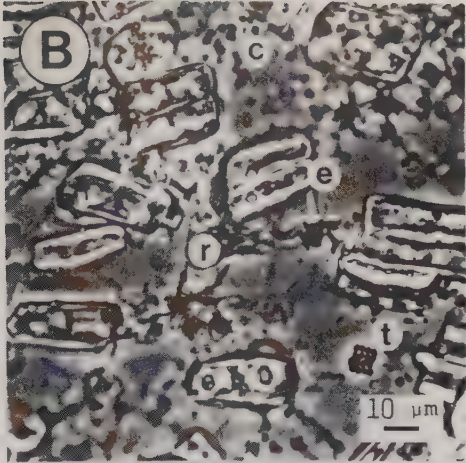
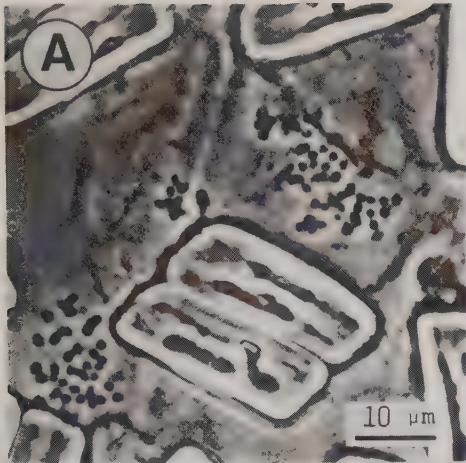
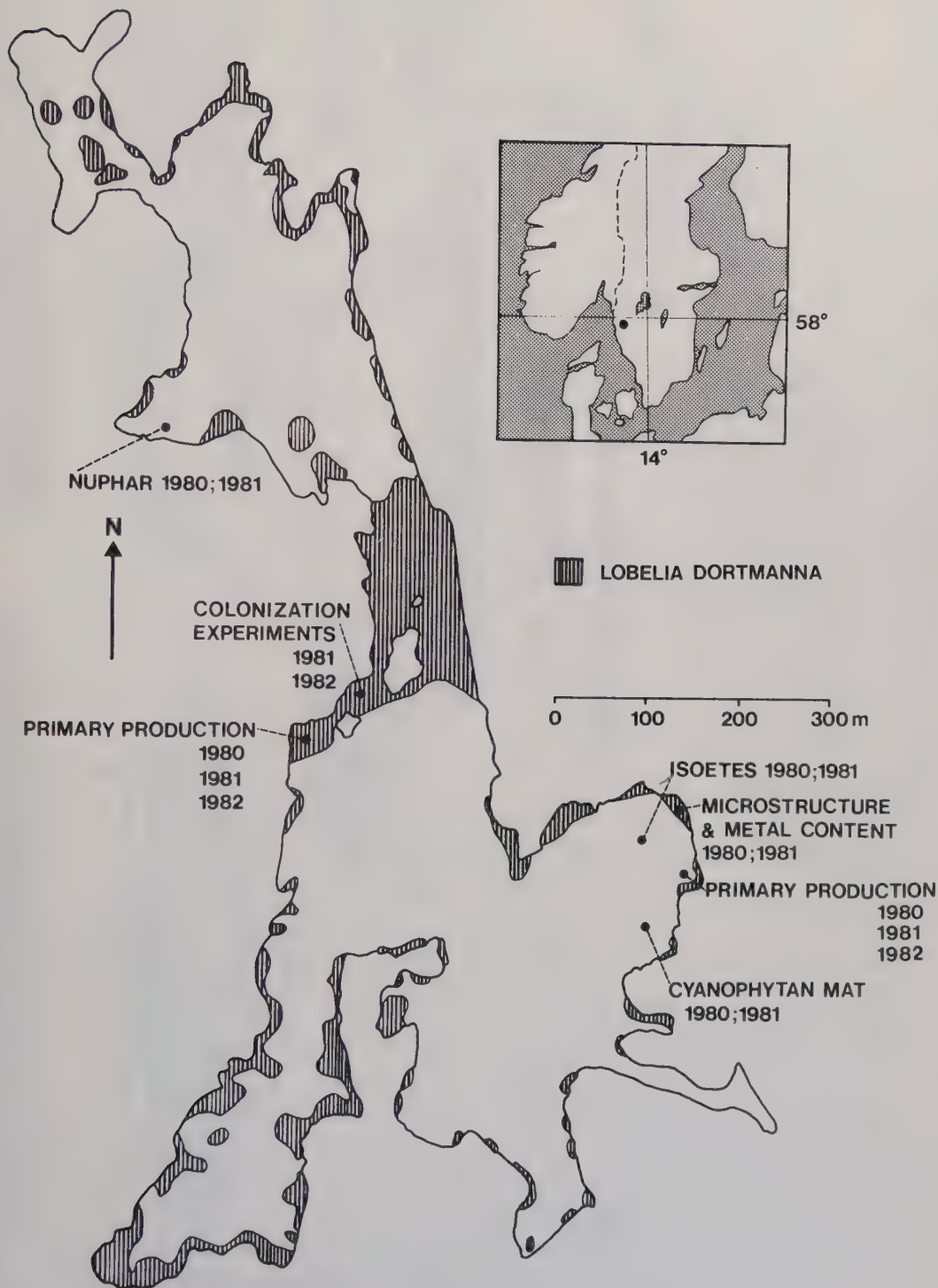


Fig. 4.



APPENDIX A



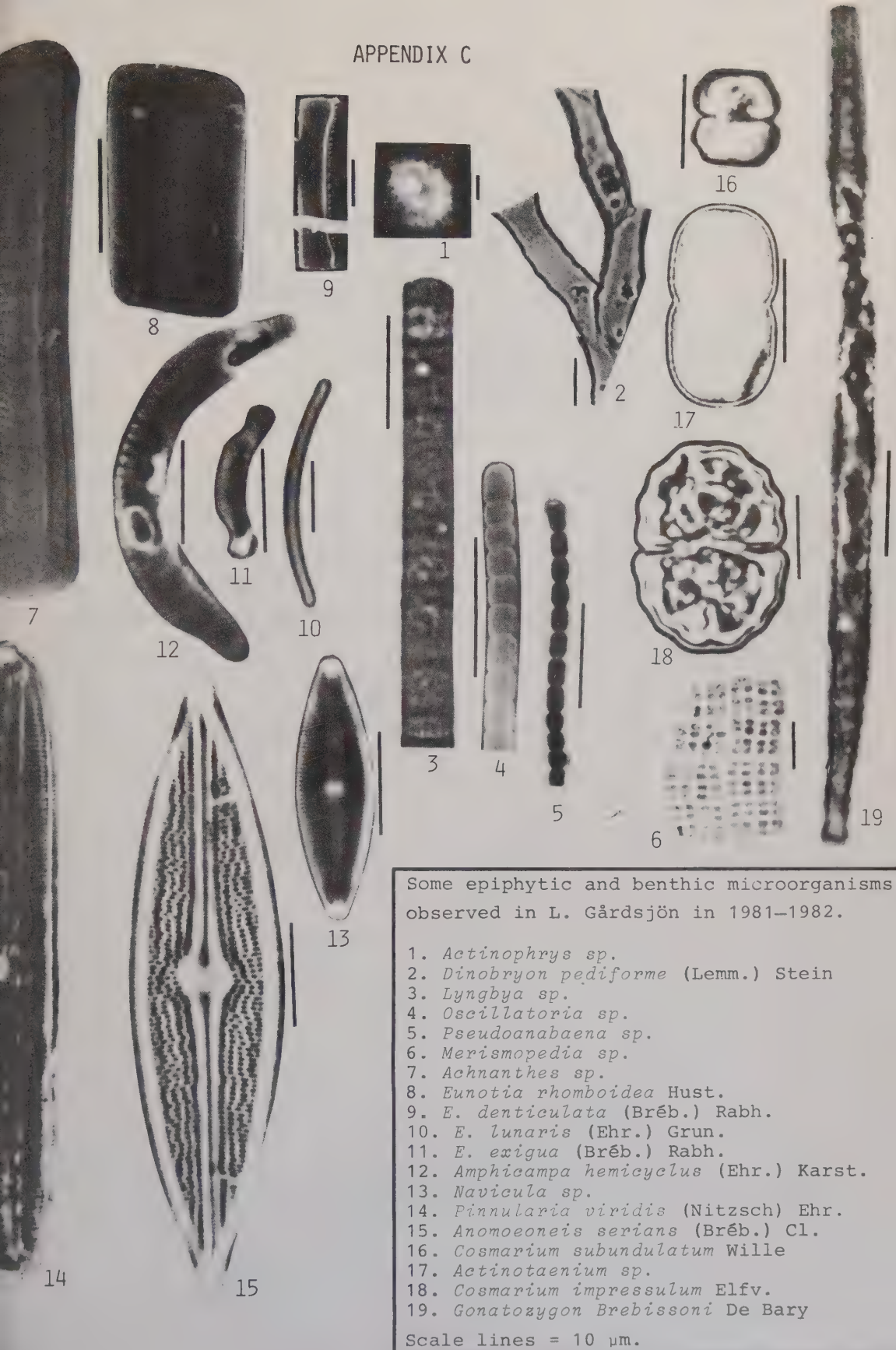
APPENDIX B

Some limnological parameters of Lake Gårdsjön*, expressed as mean values or range of values. The lake was limed in April 1982.

	1980-1981 Jan.-Dec.	1982 May-Nov.
Lake area (km ²)		0.3
Mean depth (m)		4.9
Max. depth (m)		18.5
Transparency (m)	9.5	
Colour (mgPt.l ⁻¹)	2-6	1-5
pH	4.2-4.7	7.4-7.7
Conductivity (mS.m ⁻¹)	6.2-8.1	7.6-12.2
Alkalinity (meq.l ⁻¹)	0.00	0.2-0.7
Total-P (μg.l ⁻¹)	6.2	
PO ₄ -P (μg.l ⁻¹)	3.7	
Total-N (μg.l ⁻¹)	380	
NO ₂ ⁺ NO ₃ -N (μg.l ⁻¹)	110	93-120
NH ₄ -N (μg.l ⁻¹)	56	26.3-260.0
DIC (mg.l ⁻¹)	0.7-1.2	4.5-8.6
DOC (mg.l ⁻¹)	3.6	
Total-Al (μg.l ⁻¹)	350	
Ca (mg.l ⁻¹)	1.86	7.8-14.6
SO ₄ (mg.l ⁻¹)	10.9	10.8-7.5
SiO ₄ (mg.l ⁻¹)	0.25	
Chlorophyll <i>a</i> (μg.l ⁻¹)	1.0	
Net production (g dwt.m ⁻² lake area):		
Total macrophytes	8.9	
<i>Lobelia dortmanna</i>	2.6	
<i>Lobelia</i> leaf turnover (%)	38	

* determined within the integrated Lake Gårdsjön project.

APPENDIX C



Some epiphytic and benthic microorganisms observed in L. Gårdsjön in 1981–1982.

1. *Actinophrys* sp.
2. *Dinobryon pediforme* (Lemm.) Stein
3. *Lyngbya* sp.
4. *Oscillatoria* sp.
5. *Pseudoanabaena* sp.
6. *Merismopedia* sp.
7. *Achnanthes* sp.
8. *Eunotia rhomboidea* Hust.
9. *E. denticulata* (Bréb.) Rabh.
10. *E. lunaris* (Ehr.) Grun.
11. *E. exigua* (Bréb.) Rabh.
12. *Amphicampa hemicyclus* (Ehr.) Karst.
13. *Navicula* sp.
14. *Pinnularia viridis* (Nitzsch) Ehr.
15. *Anomoeoneis seriens* (Bréb.) Cl.
16. *Cosmarium subundulatum* Wille
17. *Actinotaenium* sp.
18. *Cosmarium impressulum* Elfv.
19. *Gonatozygon Brebissoni* De Bary

Scale lines = 10 μ m.

APPENDIX D

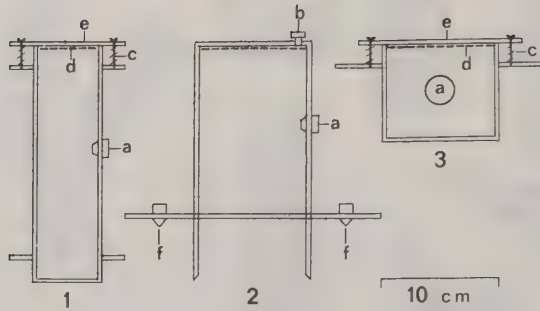
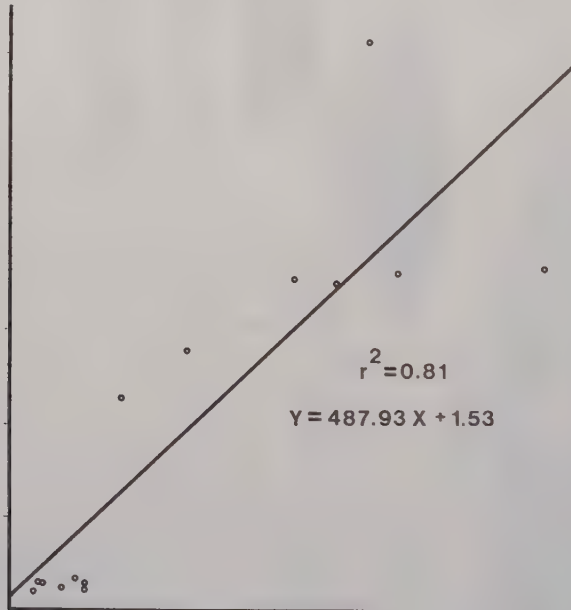


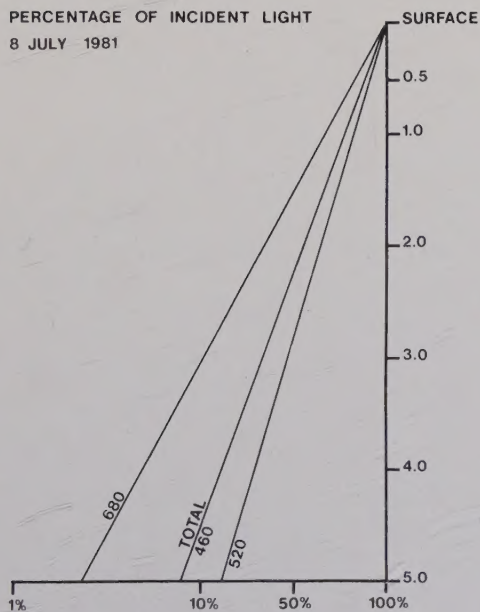
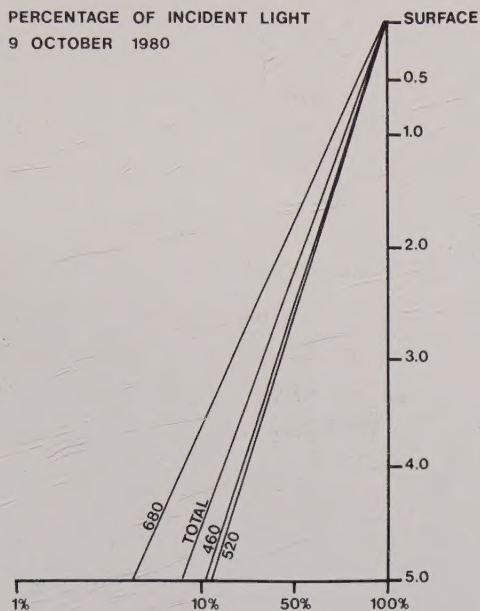
Diagram of the plexiglas chambers used for the *in situ* ^{14}C uptake experiments. (1) 450 ml, (2) 1000 ml, (3) 600 ml. (a) rubber septum, (b) screw prop to release trapped air and excess water when the chamber was inserted into the sediment, (c) screws, (d) rubber rings, (e) transparent lid, (f) weights.



Linear regression for conversion of the *Lobelia* leaf biomass (X) expressed in g dwt, to cm^2 leaf surface area (Y).

APPENDIX E

Semilogarithmic plot of light transmission in the littoral of L. Gårdsjön. Wave length is given in nannometers.



Environmetrics 1983, 1: 1-10
Environmetrics 1983, 1: 1-10

